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NOTES ON THE ANIMAL LIFE OF THERMAL WATERS IN THE YELLOWSTONE NATIONAL PARK

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The Yellowstone National Park offers ideal and unexcelled opportunities for studying the ecology of thermal waters. The following notes are based on brief and scattered observations made in July, 1930. One problem that is indirectly connected with thermal waters seems interesting but was not even touched. It is as to whether the warming of the ground by the subsurface heat in such regions as the Old Faithful district has resulted in the maintainance of a more southern fauna there than in immediately adjacent districts at the same altitude.

A great deal of the large amount of work which has been done on the animal life of American thermal waters has been based on just such short visits to one or to many springs. These visits have resulted in much valuable information but it seems that a long stay with daily and even hourly observations of selected springs or streams in such a region as the Yellowstone might add still more to our knowledge of their problems—or to the mystery of them. One reason for this is that there are often rapid changes in the thermal and other conditions of given springs or streams, changes which, if not known, would make a single observation decidedly misleading.

It is a self-evident principle of ecology that among environmental factors those that are both important in themselves and different in different places are the most influential in determining distribution. Although temperature is the evident characteristic of thermal waters, the dissolved chemicals, specific gravity and especially the recently popular p_H have been noted by the more thorough observers. Which of these is ecologically basic?

Just north of Butterfly Cone in the Old Faithful district there is a pool ("25A") somewhat more than a meter in diameter and in depth. Its banks are muddy and its temperature at the various times when it was measured was within a degree of 24°C. It was "alive" with minute Crustacea (chiefly *Simocephalus serratulus*) and there were also numerous Notonectidæ. About six meters from this pool and in the same

sort of soil was a larger (about ten meters in diameter) pool ("25B"). The temperature of its water at the edges was about 44° C. but without doubt it was warmer near the center. So far as I could determine, there was no animal life of any kind in this pool but there was a fair growth of algæ.

Water was taken from the second ("25B") pool and allowed to cool. When it had reached 24° a hundred or more of the Crustacea from the first ("25A") pool were put into it and set aside to await results. After three days all of the Crustacea, so far as I could determine, were still alive, indicating that, whatever minor or slowly-acting influence other factors may have had, the difference in temperature was very important. This was further confirmed by the reverse experiment of partly filling a large test-tube with Crustacea and water from the 24° pool and then floating this tube in the 44° one. Within less than half an hour after the water in the tube had reached the temperature of the pool all of the Crustacea were dead.

Possibly because their actions could be more easily observed, the backswimmers (Notonectidæ) were somewhat more dramatic when subjected to the same experiments. Nine of them, with 24° water from their pool, were put into an olive bottle which was then set in a shallow part of the warmer pool. In six minutes the water in the bottle had reached 35.5° and the bugs had noticeably increased their activity. Three minutes later the temperature was 38° and the bugs were not only very active but they were, for the most part, dorsal side up and trying to crawl out of the water. In three more minutes the temperature had risen to 39° and the bugs were in evident distress. When the water had reached 40° the wings of several bugs were outspread as in death; at 40.2° all were quiet except for spasmodic twitchings of legs; and at 41.5°, twenty-seven minutes after starting the experiment, all were dead.

Of course, what happens in nature is that, if a notonectid flying from pool to pool alights in one that is too warm for it, it immediately takes flight again unless the second pool is so hot as to paralyze the insect suddenly. This was demonstrated by nearly filling a bottle with water at 38°C. and putting several notonectids from the "25A" pool into it. They immediately came to the surface and tried to fly out, one succeeding, the others slipping back and trying again, only to hit against the opposite side of the bottle. When the water had cooled to 36° they seemed more content to stay in it and at 35° even fresh specimens made no attempt to escape.

Such being the case, it is quite evident that a temperature of 38° or

higher would alone keep these insects out of a pool, no matter what be the chemical content, specific gravity, or p_H. This experimenting was carried a bit further by using the Crustacea as test material. Water was taken from a large variety of hot springs in the Old Faithful district, including Beach Spring, Riverside Geyser and Old Faithful itself. These water samples were cooled and stocked with plankton from the "25A" pool. No case was found in which such plankton did not live without any apparent increase in death-rate for three days, the arbitrary length of the experiments.

The relation between temperature and the distribution of aquatic insects was beautifully shown in the very shallow water at the edge of a marshy spot draining a hot spring in the Norris district. Beetles (*Enochrus hamiltoni* and *Tropisternus californicus*) and mosquito larvæ which were abundant where the temperature was less than 37° were practically absent where, less than a meter distant, it was more than 38°. If driven by hand into the warmer water they immediately left it for the cooler, although it is quite improbable that in these cases there was any, or, at least, any noticeable-to-them, change in specific gravity or p_H.

I put one of the larger water-beetles (*Tropisternus*) with water from this pool into a tube and held the tube in a hot spring. In about a minute the temperature had reached 45.4° and the beetle was dead. A mating pair of these beetles was tested in a similar manner except that the tube was kept in the hot spring for only a few seconds at a time so that the temperature increased gradually to 45°C. One of the beetles died at 44° but the other, which at 45° had stretched its legs out ventrally in a death pose and was floating, motionless, with its dorsum and not its anal end at the surface, recovered movement as the water was allowed to cool. By the next day it was as lively as ever.

The water entering Black Sand Pool in the Old Faithful district is said to be superheated. At the margin of a small pool fed by the overflow of Black Sand the temperature of the water was only 24°C. There was no higher vegetation at this point, the bottom being small pieces of geyser "formation" slightly covered with a brown growth (algæ?). There were numerous small beetles of three families and five genera: *Bidessus affinis* and *Deronectes striatellus* of the Dytiscidæ; *Enochrus carinatus* and *Laccobius agilis* of the Hydrophilidæ; and either *Helmis divergens* or a closely related species of the Helmidæ. Less than a meter nearer the center of the pool the temperature of the water was 32° and there were no beetles. Experiments made in the manner previously

described showed that these beetles survived heating to 41° for a short time but were distinctly uncomfortable at, say, 35° and died at 45°C. It seems rather clear that temperature is a major and probably the sole inorganic factor in determining their distribution in this pool and probably elsewhere.

An exceedingly interesting lay-out was afforded by rivulets flowing from small hot springs which were located in the rather open pine forest N.E. of Solitary Geyser in the Old Faithful district. Taking one such rivulet as an example, the water as it came out of the ground had a temperature of 48°C. Since the slope was moderately steep, the rivulet, in places not 20 cm. wide, resembled the common idea of a babbling mountain brook except for its temperature. At its source the stream was much choked (entirely covered in one place) by a thick growth of stringy, slimy, matted algæ such as are characteristic of thermal waters. No animal life was found in the water at this point. It is to be expected that the algæ, as well as the flowing of the water, give it as much oxygen as the temperature allows.

Roughly 25 meters below its source the stream's temperature had dropped to about 44° C. Thermal algæ still covered the bottom but moss grew on the bank close to the water's edge. However, I still could find no animal life in the water.

Roughly 40 meters below the stream's source the current was very swift and the temperature 42°. Thermal algæ were present but not so luxuriant and there were in it the red dipterous larvæ (*Tanytarsus* sp.)[1] characteristic of thermal waters; but no other animal life was found. These larvæ can survive at least short experimental exposures to temperatures higher than 42° and probably could do so in nature. However, at even slightly higher temperatures they become active, crawl out of the muck or algæ, and swim about with bending motions of the body. In a stream such as the one under discussion this would naturally result in their going with the current and usually into cooler water. Therefore, it is probable that they were not found nearer the source of this stream, not because they could not withstand even the temperatures there but, because any even slight increase in temperature due to an increase in the volume of hot water coming out of the spring would result in their becoming active and floating down-stream into cooler water.

That this reaction of chironomid larvæ does not always result favorably was evident in the Norris Basin where a small, warm stream,

[1]These and other identifications of Diptera are by Mr. C. H. Curran; those of Coleoptera, by Mr. A. J. Mutchler; and those of lower invertebrates by Dr. W. G. Van Name.

flowing across a flat, passed through a pool kept hot by a thermal spring. The temperature of the stream as it entered the pool was 36° and as it left was 42°C. The temperature of the pool varied from place to place depending on the currents but averaged well above 55°C. On July 4 the stream was so full of wriggling red larvæ of a species of *Chironomus* near *tentans* that they were floating with the current at an average rate of 38 per minute. All were alive as they entered one side of the pool and all were dead as the current floated them out at the other side. Circumstances did not permit me to follow up the stream to see what had started this striking mass-movement of larvæ but probably it was due to the increased activity of a hot spring warming by a few degrees the water in which they were breeding.

Returning to the description of the stream in the Old Faithful district, the temperature (42°) already given as that of the stream about 40 meters below its source was taken at ten o'clock in the morning. At two o'clock that afternoon the temperature at exactly the same point was 43°, the difference possibly being due to the fact that the morning was very cloudy but in the afternoon the sun was shining on the water. There had in this case been no noticeable change in the temperature of the spring.

Approximately 60 meters from its source the stream was swift but with eddies. The temperature was 41° at about 4:00 P.M. Then there was a light shower for nearly an hour. About half an hour after the shower stopped the temperature was only 39°C. There were none of the thermal algæ which were so abundant above, unless the very short, dark growth on the pebbles was a depauperate representative. *Tanytarsus* larvæ were present and also hydrachnids which I have tentatively identified as *Thermacarus nevadensis* and a beetle, *Paracymus subcupreus*.

Approximately 75 meters from the stream's source the temperature at 5:40 P.M. (ten minutes after noting that the temperature was 39° about 15 meters farther up the stream) was 37° but it was 38° at ten o'clock the next morning and it probably reached at least 39° on clear days. Mr. Curran identifies the rather abundant red dipterous larvæ found here as *Palpomyia* sp. A small crustacean (*Hyalella knickerbockeri*) was another new element in the fauna, as was the beetle *Helmis similis*. See Table 1 for the constitution of observed fauna here and at other points along this stream.

Approximately 105 meters from the stream's source the temperature was 35.5°C. The brook seemed otherwise about as before except that

the growth on the stones was a little greener. No specimens of the hydrachnid and no *P. subcupreus* were found but a heteropteran (*Ambrysus heidemanni* Montandon, identified by Mr. R. L. Usinger) had come into the fauna. *Palpomyia* larvæ were still present.

Approximate																	
Meters from Source	Temp.	Thermal Algæ	*Tanytarsus* (Diptera)	*Thermacarus* (Hydrachnidæ)	*Paracymus* (Coleoptera)	*Palpomyia* (Diptera)	*Helmis similis* (Coleoptera)	*Hyalella* (Crustacea)	*Ambrysus* (Hemiptera)	*Tanypus* (Diptera)	Trichoptera	Ephemerida	Odonata	*Helmis divergens?* (Coleoptera)	*Simulium* (Diptera)
0	48°	×													
25	44°	×													
40	42°	×	×												
60	40°		×	×	×										
75	38°		×	×	×	×	×	×							
105	36°		×			×	×	×	×						
135	35°		×			×	×	×	×	×					
165	33°					×	×	×	×	×	×				
195	31°						×	×	×	×	×				
225	29°						×	×	×	×	×				
230	35°		×			×	×	×	×						
315	33°						×	×	×	×	×				
705	26°						×	×	×		×	×	×	×	
885	24°						×	×	×		×	×	×	×	×

Table 1.—See text for explanations.

Approximately 135 meters from the stream's source the temperature was 35.5°. The stream was still swift but not so much choked with sticks and stones, hence not so turbulent. The fauna seemed to be that of the 105-meter point, except that dipterous larvæ of the genus *Tanypus* had come in.

Approximately 165 meters from the stream's source the temperature was 33° at 2:00 P.M. As the midday sun had been shining brightly and the brook was especially exposed for some distance above this point by a windfall of trees, 33° is probably fairly close to the maximum. Sedges were growing in the water. Beetles (*Helmis similis*) and Crustacea (*Hyalella knickerbockeri*) were abundant but no *Tanytarsus* larvæ were found. Offsetting their absence were caddis larvæ as a new element in the fauna.

Approximately 180 meters from its source the stream took a winding course with a slower current among young pines. At about 195

meters the temperature was 31° at 3:30 P.M. The pebbles were fairly clear of algæ and there was no other noticeable aquatic vegetation. The fauna was chiefly made up of the heteropteron (*Ambrysus heidemanni*) and caddis larvæ of two sorts: one having a light-colored abdomen and living in fixed masses of small pebbles and one having a green abdomen and living in portable cases. There were a few *H. similis* and Crustacea but *Palpomyia* had apparently dropped out.

Approximately 225 meters from its source and a meter before it joins another, larger, and warmer stream the temperature of the stream we have been following was 29°C. in the late afternoon. There was a light drizzle of rain most of that night and at 10:30 the next morning the temperature of the water at this point was only 26.5°C. The fauna had the same elements as at the 195-meter point, although the proportions were somewhat different, the light-abdomened caddis larvæ being particularly abundant.

This joining of streams started, as will be seen, a new series in the faunal changes. When the temperature in the smaller stream a meter above the junction was only 26.5° the temperature of the larger stream at a corresponding point was 35°C. As the day was still damp and cold, it is probable that the water in the larger stream at this point often reaches at least 37°. Just below the junction, average temperature about 35°, *Tanytarsus* larvæ were very abundant. There were few *Helmis similis* and most of them were dead. Several *Ambrysus heidemanni* and several *Hyalella knickerbockeri* were found after much searching, but no caddis. In other words, it was the fauna of the smaller stream at a point about 100 meters above, where the temperature was about the same.

The temperature 30 meters below the junction of these streams was 33°; 60 meters below the junction it was 32°; and about 90 meters below the junction it was 31.5° at one time but less than an hour later, with bright sun, it was 33°C. At this point there was the fauna of the same temperature 150 meters above, except that no *Palpomyia* larvæ were taken.

Temperatures at various points below the junction were measured in rapid succession as follows: 150 meters, 32°; 210 meters, 31°; 300 meters, 30°; 390 meters, 29°; 480 meters (after tumbling down the very steep side of a hill), only 26°C. At this latter point there were filamentous algæ in the stream while yellow monkshood and other herbs crowded the bank. *Hyalella knickerbockeri*, *Helmis similis*, and the *Ambrysus* were still present but they had been joined by a worm (*Plannaria fore-*

manii), another beetle (*Helmis divergens?*), may-fly and damsel-fly larvæ, and caddis larvæ in spiral cases. *Tanypus* had apparently dropped out.

About 660 meters below the junction with the warmer stream (roughly 900 meters from the source of the stream we have been following) the temperature of the water was only 24.5°C. and the presence of *Simulium* larvæ gave the fauna a distinctly "normal brook" aspect in spite of the few remnants from the warmer upper parts. Probably the idea in that last clause should be reversed, for it is likely that the fauna of cool water goes as far into the warm as possible and that the "tension" is not from the warm into the cool.

The heteropteron, *Ambrysus heidemanni*, is one of the more interesting insects of this stream. Brues recorded it from a hot (34°) spring near Bridgeport, California, as well as from Yellowstone, the type locality. In the Yellowstone he found it "in water at 35.5° which was highly charged with silica. It would appear, therefore, that this insect occurs generally in thermal springs of moderate temperature. One of its relatives, *Naucoris cimicoides* of Europe occurs in saline water, but no other members of the family have been found in thermal springs" (Brues, 1928, Proc. Amer. Acad. Arts Sci., LXIII, p. 172).

Since Brues found it nowhere else in his extensive survey it may not really occur generally but it was certainly abundant in the Yellowstone in 1930 at a number of places where the temperature was between 25 and 35°C. It will be noted that in the stream just discussed it was found where the water was from 35 to about 39° but no warmer. Experiments in warming water into which mature specimens had been put showed that their movements became greatly accelerated at 39°C. One specimen, when raised to 41.5° for just a few seconds and then allowed to cool slowly appeared to have died. When taken out of the water it revived somewhat but was sluggish and moved only when stimulated. Put into water at 19° it became active. The temperature was then raised to 43° and allowed to drop, reaching 41.5° in a minute. The bug ceased active movements, legs outstretched and twitching slightly. In three minutes the water had cooled to 31° but the bug did not respond to mechanical stimulation. After having been taken out of the water for ten minutes it still did not move. When returned to water at 20° it moved slightly almost immediately and slowly revived until it was apparently fairly normal but sluggish.

Any increase, such as is common, in the thermal activity at the source of this stream would quickly raise the temperature at 100 meters

below. Apparently the *Ambrysus* would voluntarily start moving into cooler water if the temperature approached 39° and if the temperature reached, say, 41° the insect would lose its power of movement and be washed involuntarily to cooler water, where it would revive and continue to live unless, when the thermal activity had lessened, it crawled up-stream again. This would be true whatever the chemical factors of the environment might be. Admittedly these chemical factors may, if extreme enough, prevent it from living in water of suitable temperature but its absence from such a place at a given time proves little about the fitness of that place at that time. This is particularly true of pools which change their temperature rather markedly from time to time and from which at least the young of this species could not easily escape if the water got too hot.

Further examples of the faunistic effect of local and occasional differences of temperature were seen along the banks of the Firehole River where it was joined by the hot overflow of geysers. One such place is the outlet of Sawmill Geyser, but a more spectacular one is Riverside Geyser.

The latter shoots diagonally up-stream into Firehole River but for an hour or two just before an eruption it pours hot water into the brink of the river. When the geyser was not overflowing, the temperature of the water at the river's edge was from 19 to 22°C. When, however, the geyser was overflowing strongly, the temperature thirty feet below the overflow was greater than 50° (more than an insect can stand); fifty feet below the overflow it was 39° and eighty feet below it was 28°C. These are merely typical figures. As a matter of fact, the temperature even during a fairly constant overflow varied five degrees or more in a few minutes at a given place due to swirls in the water. The point is that the more or less sedentary insect larvæ must be prepared to withstand the maximum heat at the place in which they are living. If it gets too hot they either let go and are washed into cooler water or they die.

On the other hand, the water even at the place of overflow may be too cool during the geyser's quiescent hours for extremely thermal things, this probably explaining their absence. In fact, for some feet below the geyser the river's edge seemed to be almost lifeless. Just up-stream from the geyser, however, the normal cool-water flora and fauna flourished in spite of the fact that the geyser errupts in that direction. As was determined by standing in it, the spray is not uncomfort-

ably hot when it strikes the river and it is then, of course, both cooled and rapidly carried down-stream.

It is difficult to draw any other conclusion from these observations, which are all too scant and should be extended in detail throughout a season or longer, than that temperature is the principal inorganic environmental factor in controlling the distribution of life in these waters. While the possible lesser effects of chemical characteristics should be kept in mind and sought, only experimental evidence will prove their importance.